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Research Article

Trophic ecology and niche overlap of two sympatric species of *Rhamdia* (Siluriformes, Heptapteridae) from northeast Oaxaca, Mexico

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Abstract

The trophic ecology of fishes in the genus *Rhamdia* remains poorly reported. Here, we aim to describe the diet composition and infer the trophic levels, niche breadth, and niche overlap between *Rhamdia guatemalensis* and *Rhamdia laticauda* in northeast Oaxaca, Mexico. Fishes were sampled using an electrofishing device between 2016 and 2017. We calculated the Quotient index and the diet composition was analyzed using the percentage of the Index of Relative Importance (%IRI) to analyze possible ontogenetic and sexual differences on feeding ecology. We then calculated the trophic niche breadth using the Levins´ standardized index (B_A). Trophic levels (TL_k) of each species were calculated using the trophic index and trophic niche overlap using Pianka´s index (O_{jk}). The results indicate that both species are carnivorous and tend to prey on aquatic insects, with *R. guatemalensis* feeding on nine different orders of animals and *R. laticauda* displaying a broader diet spectrum, encompassing 19 orders. Our data showed ontogeny and sex differences in the trophic ecology of *R. guatemalensis*. They were secondary consumers (TL_k > 3) and showed a specialized diet (B_A < 0.4). We found evidence of trophic niche partitioning between adults (O_{jk} = 0.40) and females (O_{jk} = 0.42). Our results highlight the fundamental role of this species in the area as a carnivorous/insectivorous, predatory fishes, secondary consumers, and biological control for Diptera, Ephemeroptera, and Megaloptera. Both species minimize the trophic overlap through food resource partitioning mediated by fish body size. Additionally, adults and females consume different prey, which allows the coexistence of closely related species. Our findings regarding trophic ecology could be crucial for devising conservation and management plans for these particular *Rhamdia* species.

Key words: Coexistence, diet, feeding ecology, freshwater fishes, natural history, niche breadth

Introduction

Ecological differences are essential to coexistence, and closely related, sympatric (co-occurring) species need to differ in at least one of the three dimensions of the ecological niche (i.e., temporal, spatial, and trophic) to avoid competition (Pianka 1973; Schoener 1974). The trophic dimension is the most important factor in the confirmation of the ecological niche (Krebs 1999; Bolnick et al. 2003), and in fishes, it can be analyzed through the analysis of stomach contents data (Hyslop 1980; Amundsen et al. 1996; Cortés 1997). Data on the trophic ecology of fishes is essential to understanding their role in the habitat, evolutionary biology, natural history, as well as for developing management and conservation strategies (Gerking 1994; Amundsen et al. 1996; Cortés 1997). Additionally, studies on trophic niche differentiation are crucial for exploring interspecific competition and stable coexistence among morphologically similar sympatric species (Brazil-Sousa et al. 2009; Silva et al. 2012; Bonato and Fialho 2014). Sympatric species can adjust their resource use to minimize niche overlap (Pianka 1974), a phenomenon known as resource partitioning (Schoener 1974). The partitioning of food resources can be influenced by various factors such as habitat, sex, and ontogeny (Ross 1986). It is imperative to consider one of these factors when studying the mechanism of coexistence among closely related species (Bonato and Fialho 2014).

The genus *Rhamdia* Bleeker, 1858 (Siluriformes, Heptapteridae), is found in almost every freshwater environment in the Neotropical region from southern Mexico to central Argentina (Hernández et al. 2015; Bockmann and Slobodian 2017; Thomas and Sabaj 2020). However, aspects of its natural history are poorly known (Bockmann and Slobodian 2017; Thomas and Sabaj 2020), and few quantitative data have been reported on the trophic ecology of the genus *Rhamdia*, with most studies focusing on *Rhamdia quelen* (Quoy and Gaimard 1824) (Brazil-Sousa et al. 2009; Kütter et al. 2009; Pagotto et al. 2011; Olaya-Nieto et al. 2012; Silva et al. 2012; Bonato and Fialho 2014; Villares-Junior and Goitein 2015; López-Rodríguez et al. 2019). *Rhamdia* catfishes are nocturnal and show crevice-seeking habits, with the vast majority of species sharing similarities in body shape, color pattern, and habitat use (Miller 1984; Miller et al. 2005; Ribolli et al. 2017).

So far, seven species of *Rhamdia* are known from Mexico (Perdices et al. 2002; Miller et al. 2005; Hernández et al. 2015). The Pale catfish *Rhamdia guatemalensis* (Günther 1864) and the Filespin chulín *Rhamdia laticauda* (Kner 1857), which occur together in the southern Tehuacán-Cuicatlán Biosphere Reserve (TCBR), Mexico (Martínez-Ramírez et al. 2013; Julián-Caballero et al. 2017), were selected for a study of trophic ecology. *Rhamdia guatemalensis* is distributed on both the Pacific and Atlantic slopes, extending from southern Mexico to the trans-Andean region of Colombia (Hernández et al. 2015), while *R. laticauda* inhabits the waters of the Atlantic slope from Río Jamapa, Veracruz, Mexico, to central Panama (Perdices et al. 2002). Due to this distribution, sympatry exists between these two catfishes at many Central American sites (Miller 1984; Perdices et al. 2002; Hernández et al. 2015), offering an excellent opportunity to study trophic resource partitioning under such ecological conditions. Both species are classified as Least Concern by the IUCN (Arroyave 2019; Schmitter-Soto 2019). However, some populations may be threatened by water pollution, water extraction for human activities, habitat degradation, and invasive species (Martínez-Ramírez et al. 2013; Julián-Caballero et al. 2017). In

Mexico, *R. guatemalensis* is listed as "subject to special protection" (Pr) under the Official Mexican Legislation NOM-ECOL-059-SEMARNAT-2010 (SEMARNAT 2019), while *R. laticauda* is not included. Both species play a crucial role in the food chain, acting as both prey (Solís and Guerrero 2016; Lavariega et al. 2020; Carranza and Anderson 2023) and predators (Schmitter-Soto 1998; Pichler and Schiemer 2008), and are important food resources for local human communities (Martínez-Ramírez et al. 2013; Julián-Caballero et al. 2017).

Previous research in Southern Mexico has reported that *R. guatemalensis* exhibits a diverse and opportunistic diet that encompasses aquatic invertebrates, detritus, fishes, terrestrial arthropods, and terrestrial plant remains (Chávez-Lomelí et al. 1989; Schmitter-Soto 1998; Soto-Galera 2006; Pichler and Schiemer 2008; Anzueto-Calvo et al. 2013), whereas *R. laticauda* primarily subsists on aquatic insects and decapods in the Mexican state of Chiapas (Soto-Galera 2006; Anzueto-Calvo et al. 2013). These studies have shown that the diet of these species varies based on their size classes (Soto-Galera 2006; Anzueto-Calvo et al. 2013). However, there are no available studies describing sexual differences in diet for either of these species. Furthermore, details regarding niche breadth, trophic levels, and resource partitioning between these species remain unexplored.

To fill these knowledge gaps, we analyzed quantitatively the overall diet composition of *R. guatemalensis* and *R. laticauda*, and compared the dietary composition between size classes and sexes. We determine the niche breadth and trophic levels to quantify the degree of dietary specialization and to determine their positions within the food web, respectively. Finally, we assess the overlap in food items between the species to examine possible feeding mechanisms that allow them to coexist. We propose that differences in the consumption of prey items could be attributed to food resource partitioning between these coexisting species.

Methods

Study area and sampling sites

We sampled *Rhamdia* individuals between October-November 2015 and February-March 2016, using an electrofishing device in 21 sites in two dryland streams, the Río Salado and Río Grande, both tributaries of the Papaloapan River within the southern TCBR, northeast of Oaxaca State, Mexico (Fig. 1). All these records were provided by Martínez-Ramírez and CONABIO (2023). The prevailing climates throughout the reserve area are warm, dry, or arid, with mean annual temperature ranging from 22 °C to 24 °C and annual precipitation varying from 400 mm to 600 mm (López-López et al. 2019). The main types of vegetation include deciduous tropical forest, oak forest, xeric shrubland, and cacti (López-López et al. 2019). Samples were collected under permit SGPA/DGVS/09813/15 issued by the Mexican Ministry of Environment and Natural Resources (Secretaría de Medio Ambiente y Recursos Naturales, SEMARNAT). The analyzed material (Suppl. material 1) is housed in the Collection of Continental Fish at the CIIDIR Unidad Oaxaca IPN, Mexico (OAX.PEC.122.0302) and was preserved in 90% ethanol.

In the laboratory, each individual was identified using identification keys (Hernández et al. 2015). Standard length (SL; mm) and body weight (W; g) were recorded using a Mitutoyo digital caliper (precision of 0.01 mm) and digital balance (precision of 0.0001 g). Specimens were dissected to obtain the food

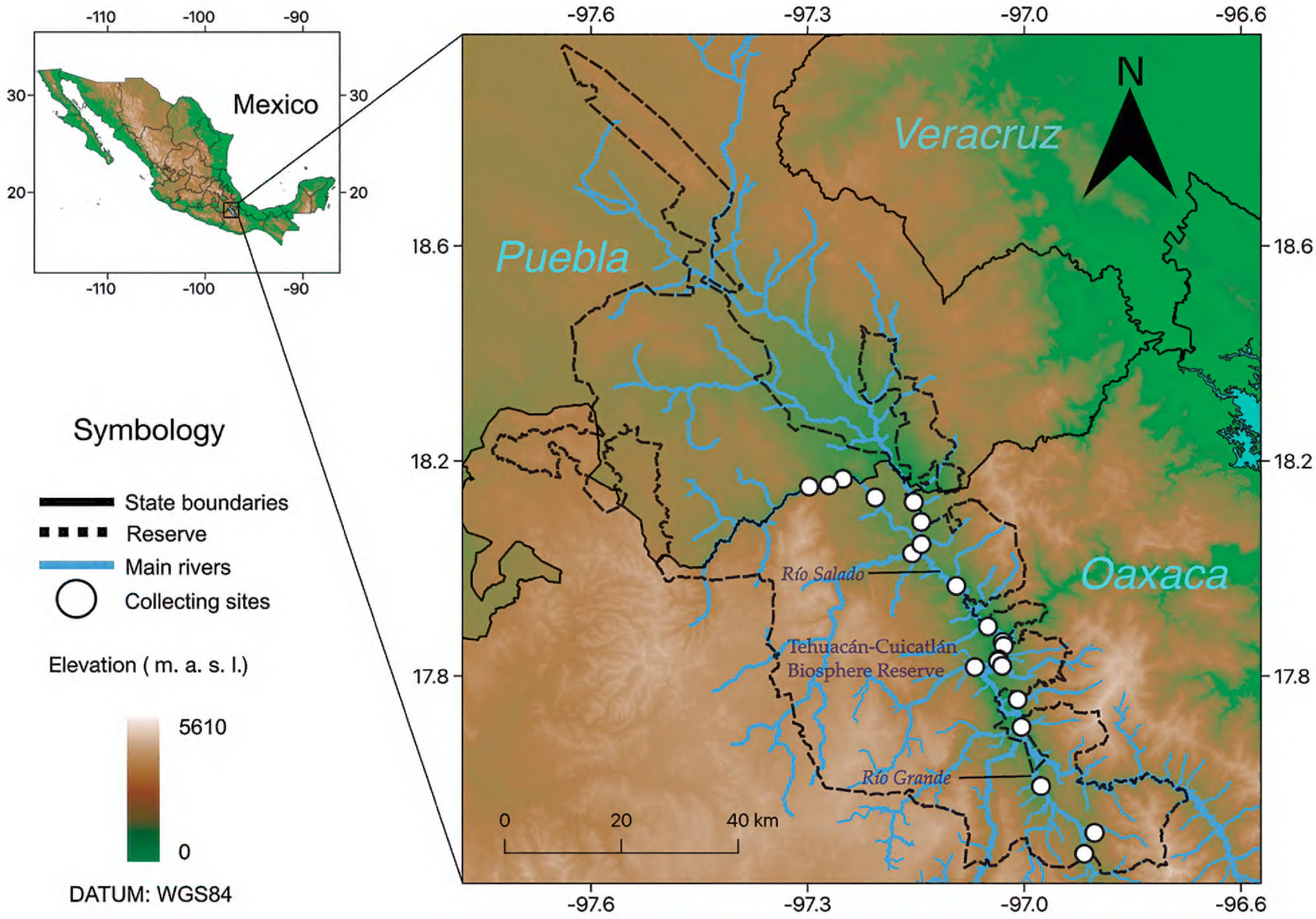

Figure 1. Collecting sites of *Rhamdia* specimens from the Tehuacán-Cuicatlán Biosphere Reserve in Oaxaca, Mexico. Map prepared using QGIS 2.6.1. (QGIS Development Team 2023).

contents of the stomach and intestine. We also measured intestinal length (IL; mm). The stomachs and intestine were stored in labeled glass flasks (25 ml) with 70% ethanol for further analysis. The sex was determined through direct examination of the gonads, however, in some individuals, it was impossible to identify, thus, they were grouped as undifferentiated. To analyze ontogenetic changes in the diet, fishes were classified according to maturation stage data (Nikolsky 1963) and SL (unpublished data). Adult females were defined as > 124.5 mm for *R. guatemalensis* and > 95 mm for *R. laticauda*, while adult males were defined as > 83.5 mm for *R. guatemalensis* and > 70.9 mm for *R. laticauda*. Specimens below these SL were considered juveniles.

Prey items were sorted using a stereomicroscope (Carl Zeiss Stemi 2000-C), identified to the lowest taxonomic level possible (Suppl. materials 2, 3), and then counted and weighed (Sartorius N° TE214S, ± 0.0001 g).

To characterize the diet of both species, the Intestinal Quotient (IQ) was calculated following Barbieri et al. (1994). Fishes can be classified based on their IQ values: carnivores with an IQ less than 1, omnivores with an IQ between 1 and 3, and herbivores with an IQ greater than 3 (Barbieri et al. 1994).

We analyzed the diet composition of *R. guatemalensis* and *R. laticauda* (Suppl. material 4) according to the Index of Relative Importance IRI (Pinkas et al. 1971), which incorporates the percentage frequency of occurrence (%FO), percentage number (%N), and gravimetric (%P) data. The results are expressed as the percentage of each prey category %IRI (Cortés 1997) using the dietR

package (Borstein 2020). We plotted the species-prey networks consumed by *R. guatemalensis* and *R. laticauda* using %IRI data and the bipartite package (Dormann et al. 2009).

Trophic niche breadth for each species, gender, and size-class (using %N) was calculated based on Levin´s niche breadth index (*B*) using the RInSp package (Zaccarelli et al. 2013), standardized (B_A) on a scale from 0 to 1 (Hurlbert 1978). Values close to 0 indicate a specialized diet, while values close to 1 indicate a generalist diet (Hurlbert 1978).

Trophic levels (TL_k) for each species were calculated using the trophic index (Cortés 1999) to determine their positions within the food web, defined as: $TL_k = 1 + (\sum_{j=1}^{n} P_j \times TL_j)$, where *n* is the total number of prey categories, P_j is the proportion of each prey category (using %IRI) in the overall diet, TL_j is the trophic level of each prey category *j*. We used prey items with default trophic values sourced from FishBase (Froese and Pauly 2023) and obtained from the dietR package (Borstein 2020). Three prey categories (fish, gastropods, and insects) were used to calculate TL_k for *R. guatemalensis*, while for *R. laticauda* we used eight prey categories: fish, herps (anura), ostracods, crabs, gastropods, arachnida, insects, and bivalves. Establishing that $TL_k = 1$ correspond to producers, $TL_k = 2$ correspond to primary consumers; and $TL_k = 3$ corresponds to secondary consumers (Cortés 1999).

We compared the diet between the species, genders, and size classes using Pianka´s Index (Pianka 1973) based on the %IRI, defined by the following equation (Pianka 1973):

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} . p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \cdot \sum_i^n p_{ik}^2}}$$

Where O_{jk} y O_{kj} = the niche overlap index between the species *j* (*R. guatemalensis*) an *k* (*R. laticauda*); p_{ij} = Proportion of the resource type *i* relative to the diet of species *j*; p_{ik} = Proportion of resource type *i* relative to the diet of species *k*; and *n* = Total number of resource categories. This index ranges between 0 (no food items in common) and 1 (complete overlap) (Pianka 1973). The figures were created with the ggplot2 package (Wickham 2016) and Cairo package (Urbanek and Horner 2023).

Statistical analysis

We tested for differences in SL, W, and IL between the species using a Mann-Whitney U test. All identifiable prey items were later categorized into five functional feeding groups: collectors, predators, filterers, shredders, and scrapers (Cummins 1973; Ramírez and Gutiérrez-Fonseca 2014), and vertebrates for the statistical analyses. Chi-square tests were used to assess differences in prey categories between sexes and size classes for each *Rhamdia* species (Zar 2010). This technique allows for the identification of the rows (prey types) and columns (e.g., predators, sex, or ontogenetic group) that are most responsible for the dietary differences (Crow 1982; Cortés 1997). Terrestrial prey items were excluded from the analyses to avoid cells with expected frequencies < 5 (Sokal and Rohlf 2009).

We performed null model analyses to test whether the observed niche overlap differs from what would be expected by chance (algorithm = RA3, permutation = 1000) using the EcoSimR package (Gotelli et al. 2015). All statistical analyses were performed using R Statistical Software version 4.2.3 (R Core Team 2023) with the significance level set to $P < 0.05$.

Results

We found significant difference in SL ($U = 15748$; $P < 0.05$), W ($U = 15614$; $P < 0.05$), and IL ($U = 5047$; $P < 0.05$) between the species. The mean IQ obtained (using all specimens) for *R. guatemalensis* was 0.69 and 0.59 for *R. laticauda*, with IQ < 1 for both sexual and ontogeny groups (Table 2), indicating that both species are classified as carnivores. We analyzed the stomach contents of 72 specimens of *R. guatemalensis* (27 females, 32 males, and 13 undifferentiated) and 112 of *R. laticauda* (52 females, 56 males, and 4 undifferentiated). We identified nine prey orders for *R. guatemalensis* and 19 for *R. laticauda* (Table 2). The most important orders in the diet of the overall composition of both species were Diptera, Ephemeroptera, Megaloptera, and Trichoptera (Fig. 2). Diptera was the most important prey order for *R. guatemalensis* (42.2%IRI), followed by Megaloptera (29.80%IRI), and Ephemeroptera (22.3%IRI). For *R. laticauda*, the most important category in the diet was Ephemeroptera (50.1%IRI), followed by Diptera (37.7%IRI). The TL_k obtained (using all specimens) for *R. guatemalensis* was $TL_k = 3.25$ and $TL_k = 3.19$ for *R. laticauda*, indicating their positions as secondary consumers within the food web.

The diet composition of both species varies as they grow (Table 2). *Rhamdia guatemalensis* showed an increased proportion of Cyprinodontiformes in adult specimens, while *R. laticauda* showed an increase in Decapoda, Characiformes, and Cyprinodontiformes. Significant differences in diet were found between size classes for *R. guatemalensis* (Chi = 88.7; df = 4; $P < 0.05$) and *R. laticauda* (Chi = 17; df = 5; $P < 0.05$).

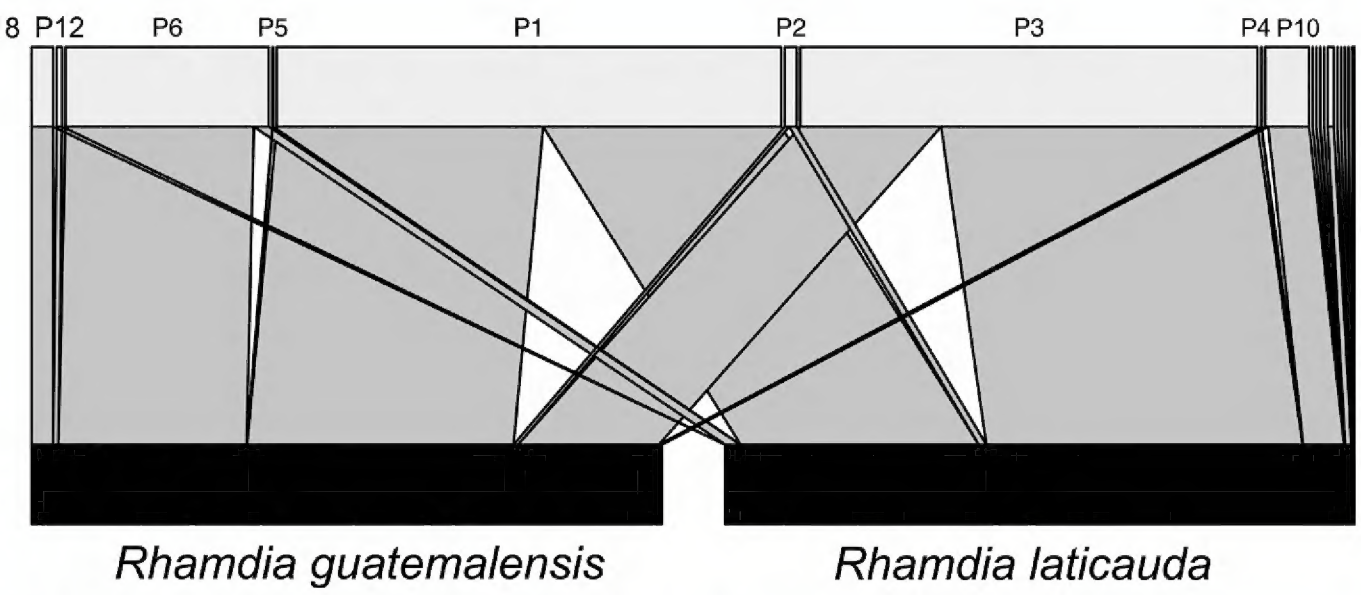

Figure 2. Species-prey network consumed by two *Rhamdia* species. The vertices sizes are proportional to the number of interactions according to %IRI data. P1 = Diptera, P2 = Coleoptera, P3 = Ephemeroptera, P4 = Trichoptera, P5= Hymenoptera, P6 = Megaloptera, P10 = Lepidoptera, P12 = Bassommatophora, and P18 = Cyprinodontiformes. For the rest of the prey orders see Table 2.

Dietary difference in %IRI between sexes were marked in *R. guatemalensis*, but not in *R. laticauda*. Female specimens of *R. guatemalensis* consumed a greater proportion of Megaloptera and Cyprinodontiformes compared to males (Table 2). In contrast, *R. laticauda* females only showed a higher proportion of Diptera and Ephemeroptera compared to males (Table 2). Significant difference in the diet were found between sexes for *R. guatemalensis* (Chi = 61; df = 4; $P < 0.05$), but no significant differences were found for *R. laticauda* (Chi = 8.8; df = 5; $P > 0.05$). The overall trophic niche breath was $B_A = 0.22$ for *R. guatemalensis* and $B_A = 0.12$ for *R. laticauda*, with $B_A < 0.4$ for both sexual and ontogeny groups (Fig. 3). There was a significant trophic overlap between juveniles ($P < 0.05$), with evidence of food partitioning between adult and female specimens ($P > 0.5$) (Fig. 4).

Discussion

We present data on morphometric and trophic niche separation between *R. guatemalensis* and *R. laticauda*, which co-occur in the TCBR, supported by evidence of body measurements (SL, W, and IL) and analysis of stomach contents data. *Rhamdia guatemalensis* and *R. laticauda* differ significantly in standard length and body mass (Table 1), which could avoid direct overlap in food and microhabitat use (Gerking 1994; Wootton 1999). A previous study indicated that these fishes show a negative allometric growth pattern and uniform body shape (Julián-Caballero et al. 2017); however, our data suggest that at the species level, *R. guatemalensis* is larger in terms of standard length and weight compared to *R. laticauda*. This information could be useful for accurate identification in the field, since it is often collected in the same sites in TCBR (Martínez-Ramírez et al. 2013; Julián-Caballero et al. 2017) and at many Central American sites (Hernández et al. 2015).

The mean IQ values ($IQ < 1$) recorded for both species in all samples (Table 2) suggest carnivorous habits. Fishes with carnivorous habits typically have shorter intestines compared to herbivorous or omnivorous fishes, presumably due to lower food ingestion amounts and higher quality, resulting in relatively rapid digestion (Pouilly et al. 2003; Becker et al. 2010; Olaya-Nieto et al. 2012). Our results confirm previous findings on the diet composition of these species in other Mexican states (Chávez-Lomelí et al. 1989; Schmitter-Soto 1998; Soto-Galera 2006; Anzueto-Calvo et al. 2013) and Costa Rica (Bussing 1998; Pichler and Schiemer 2008).

Table 1. Sample size and range of body measurements for morphometric comparison and trophic analysis in two *Rhamdia* species.

Species	Samples (*n*)	Range of standard length (mm)	Range of weight (g)
Rhamdia guatemalensis	Total (*n* = 124)	40.56–213.05	0.87–105.01
	Males (*n* = 32)	59.08–183.27	2.55–61.34
	Females (*n* = 28)	49.46–213.05	1.62–105.01
	Undifferentiated (*n* = 13)	40.56–70.73	0.87–3.38
Rhamdia laticauda	Total (*n* = 210)	37.80–133.40	0.67–33.12
	Males (*n* = 57)	57.39–126.71	2.59–24.02
	Females (*n* = 52)	56.46–133.40	2.08–33.12
	Undifferentiated (*n* = 4)	44.00–50.53	1.00–4.10

Table 2. Composition of the diet of *Rhamdia guatemalensis* and *Rhamdia laticauda* expressed as the percentage of the Index of Relative Importance (%IIR). T = Total diet, J = Juvenile, A = Adult, F = Female, and M = Male. No = total number of specimens with food in the stomach and intestine, IQ = Intestinal Quotient, and B_A = Levins´ standardized index.

Prey source	T	J	A	M	F	T	J	A	M	F
Bassommatophora	0.86	0.04	2.06	0.10	1.90	0.01	–	0.03	0.05	–
Veneroida	–	–	–	–	–	0.01	–	0.01	0.01	–
Araneae	–	–	–	–	–	0.01	0.08	–	–	0.05
Trombidiformes	–	–	–	–	–	0.02	0.01	0.03	0.01	0.04
Podocopida	–	–	–	–	–	0.30	0.02	0.89	1.15	0.04
Decapoda	–	–	–	–	–	0.10	–	0.23	0.21	0.14
Coleoptera	0.70	0.13	2.63	1.60	0.69	1.20	0.93	1.61	1.23	1.52
Diptera	42.20	41.36	32.82	48.90	28.36	37.7	37.26	36.92	35.85	39.47
Ephemeroptera	22.30	46.95	2.77	20.00	7.26	50.1	53.70	47.35	47.63	50.14
Hemiptera	0.03	0.02	0.05	–	0.22	0.07	0.19	0.03	0.02	0.19
Hymenoptera	0.07	–	0.40	0.30	0.04	0.040	0.04	0.03	0.02	0.08
Lepidoptera	–	–	–	–	–	0.017	0.05	0.01	0.01	0.04
Megaloptera	29.80	9.39	49.44	28.60	48.52	2.40	2.23	2.76	3.79	1.76
Odonata	–	–	–	–	–	1.00	0.18	2.17	1.92	0.56
Plecoptera	–	–	–	–	–	0.02	0.06	0.01	0.01	0.04
Trichoptera	0.47	2.07	0.16	0.60	0.71	6.50	5.25	7.66	7.68	5.92
Anura	–	–	–	–	–	0.006	–	0.02	0.07	–
Cyprinodontiformes	3.40	0.05	9.66	0.10	12.30	0.014	–	0.05	0.07	–
Characiformes	–	–	–	–	–	0.062	–	0.20	0.31	–
No	72	38	34	32	28	112	51	61	56	52
IQ	0.69	0.55	0.59	0.64	0.79	0.59	0.41	0.45	0.58	0.62
B_A	0.22	0.18	0.26	0.18	0.39	0.12	0.15	0.15	0.15	0.14

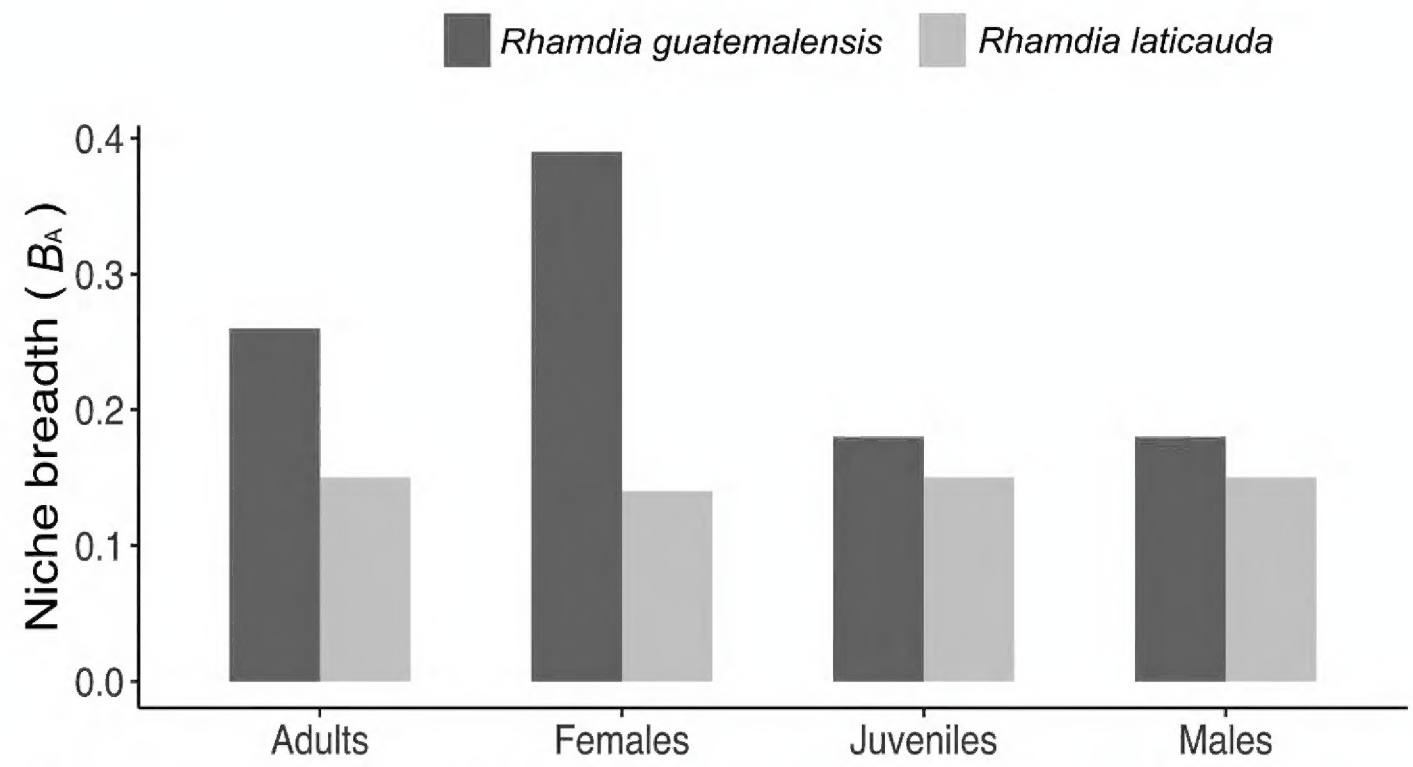

Figure 3. Niche breadth of two *Rhamdia* species calculated by size classes and sexes.

Additionally, our results align with the carnivorous habit reported for *R. quelen* (IQ range 0.65–0.76) in Brazil (Barbieri et al. 1994; Becker et al. 2010) and Colombia (Olaya-Nieto et al. 2012). Most of Heptapteridae species showed a carnivorous feeding habit, with aquatic invertebrates and fishes being the fundamental dietary items of some species (Pichler and Schiemer 2008; Mazzoni et al. 2010; Pagotto et al. 2011; Bonato and Fialho 2014; López-Rodríguez et al. 2019). Heptapteridae species can vary greatly in their fish consumption; for instance, *R. quelen*, has been reported to have values greater than 81%IIR (Olaya-Nieto et al. 2012), while for *Imparfinis usmai*, the value is less than one (Villa-Navarro et al. 2014).

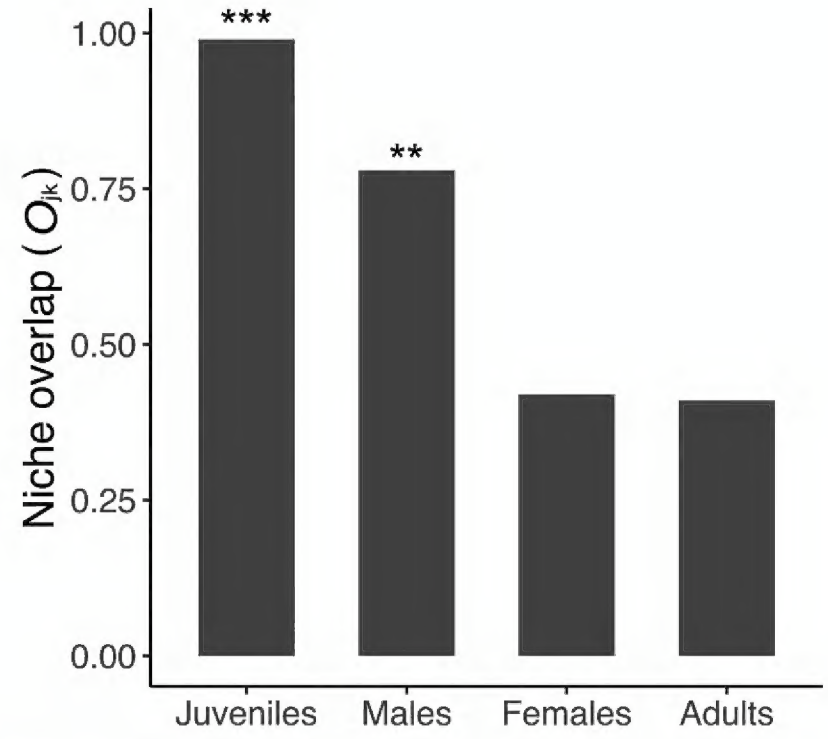

Figure 4. Niche overlap based on Pianka index (O_{jk}) between size classes and sexes of *Rhamdia guatemalensis* and *Rhamdia laticauda*. Significant codes: *** indicates P < 0.001 and ** indicates P < 0.01.

The diet composition of *R. guatemalensis* and *R. laticauda* in this area can be interpreted as aquatic invertivores, according to Goldstein and Simon (1998), and could behave as predatory fishes, as suggested by Fagade (1983). Our data showed that *R. laticauda* preys on a wide variety of fishes, anurans, ostracods, crabs, gastropods, arachnids, insects, and bivalves, while *R. guatemalensis* primarily preys on gastropods, insects, and fishes. We identified three insect orders crucial to the diets of both species based on %IRI from different samples (Table 2), Diptera, Ephemeroptera, and Megaloptera.

Larvae of lower Diptera vary in length from a few millimeters to many centimeters, depending on the species (Fusari et al. 2018), and are found in gravel, trunks, branches, and stems, living in colonies with slow movements, making them easy prey for predators (Merritt et al. 2008). Ephemeroptera are significant components during their nymph stages and are constantly present throughout the year (Barber-James et al. 2008; Merritt et al. 2008), serving as essential prey for Heptapteridae species (Rondineli et al. 2011; Villa-Navarro et al. 2014; Do Carmo and Souza 2019). Megaloptera larvae are known to be hunted by Heptapteridae species (Brazil-Sousa et al. 2009; Mazzoni et al. 2010; Bonato and Fialho 2014). Larval corydalids may be large (20–80 mm in body length) and are conspicuous benthic components in lotic waters, where they can achieve high abundances in specific ecosystems and regions, making them important prey for predatory fishes (Ardila-Camacho and Contreras-Ramos 2018; López-López et al. 2019; Rivera-Gasperín et al. 2019).

The obtained trophic level values (TL_k > 3) for *R. guatemalensis* and *R. laticauda* suggest that they are secondary consumers. These results are close to the values reported for the order Siluriformes (TL_k = 3.42) (Romanuk et al. 2011) and smaller than those reported for *R. quelen* (TL_k = 3.9) (Froese and Pauly 2023), the largest species of *Rhamdia* (> 300 mm SL) (Bockmann and Slobodian 2017). This could be explained by the positive relationship between trophic level and body size in carnivorous fishes (Romanuk et al. 2011; Keppeler et al. 2020). This data highlights the ecological role of *R. guatemalensis* and *R. laticauda* in the TCBR, recorded here for the first time using stomach content data, representing an advance in the knowledge of the natural history of genus *Rhamdia*.

Our analysis indicates that the diet composition of both species varies depending on size, with an increase in the proportions of fishes for *R. guatemalensis* and fishes and decapods for *R. laticauda* as they grow (Table 2). Our results align with those reported in other studies for *R. guatemalensis* and *R. laticauda* in different states of Mexico (Soto-Galera 2006; Anzueto-Calvo et al. 2013), as well as for other members of Heptapteridae (Moraes et al. 2013; Bonato and Fialho 2014). As fish grow, their diversity and trophic range expand due to morphological limitations in capturing certain foods. Juveniles are unable to consume fishes and decapods because of their limited capacity and size to capture and process these types of prey. The ability of juveniles to consume fishes and decapods may be restricted by the size of their mouth opening (Gerking 1994; Wootton 1999). This diet variation by size of the fish is also related to the growth and maturity stages of these species, because the energy and nutritional requirements may differ throughout their life history as predators (Gerking 1994; Wootton 1999).

We found a dietary difference between sexes in *R. guatemalensis*, but not in *R. laticauda*. In the case of *R. guatemalensis*, this difference could be related to a broader range of body measurements (Table 1) or different IQ values found in females, and niche breadth values between the sexes (Table 2). In contrast, data obtained for *R. laticauda* suggest that there is less variation in the range of body measurements or alimentary index (Tables 1, 2). Diet difference between sexes in genus *Rhamdia* has not been published. However, variation in diet between sexes in fishes may occur due to differences in behavior and energy allocation (Gerking 1994; Wootton 1999), or it might be influenced by size of individuals or sexual size dimorphism (Gerking 1994). However, this information requires further investigation because no sexual size dimorphism has been published for Heptapteridae species (Bockmann and Slobodian 2017).

Values of Levins´ standardized index (B_A < 0.4) suggest that both species showed a tendency towards dietary specialization (Grossman 1986; Bonato and Fialho 2014), probably associated with the morphological adaptations and a benthophagous feeding habit. Similar dietary specialization has been reported in *R. quelen* (Pouilly et al. 2006; Brazil-Sousa et al. 2009; Kütter et al. 2009; Olaya-Nieto et al. 2012; Silva et al. 2012; Bonato and Fialho 2014; López-Rodríguez et al. 2019). However, individuals of the genus *Rhamdia* could be adapted to exploit prey that becomes abundant seasonally, locally, or due to stochastically limitations to a narrow range of resources in their environment (Villares-Junior and Goitein 2015). To consume prey from the benthos, *R. guatemalensis* and *R. laticauda* possess three pairs of sensory and tactile barbels, which are used for detection (through taste buds) and selection of prey before ingestion (Miller 1984; Kobelkowsky and Castillo-Rivera 1996; Wilkens 2001; Hernández et al. 2009). Understanding the dietary specialization or habitat of organisms is crucial for comprehending population declines in specific species and implementing effective conservation measures (Costa et al. 2015). Specialist species often have very specific diets and habitat requirements, making them more vulnerable to environmental fragmentation and food depletion. Consequently, they are more prone to extinction compared to generalist species (Costa et al. 2015). Preserving the rivers and streams in this area is essential because certain orders of insects (Ephemeroptera, Plecoptera, and Trichoptera) that are part of the diet of *Rhamdia* species are sensitive to contamination (Barber-James et al. 2008; Merritt et al. 2008).

The Pianka index indicated a low to high dietary overlap, primarily driven by the consumption of Diptera and Ephemeroptera (Fig. 2), two abundant orders of aquatic macroinvertebrates in the study area (López-López et al. 2019), suggesting opportunistic exploitation. According to Taylor et al. (2011), if the composition and overlapping of the diets is based on very abundant trophic resources, then it is most likely that opportunistic exploitation of these resources is occurring. This is consistent with the previous knowledge of *Rhamdia* species, which exhibit an opportunistic diet pattern and high food plasticity that seems to be the strategy employed (Miller 1984; Wilkens 2001; Wilkens and Strecker 2017). Thus, their diet varies depending on food availability and geographical location (Miller 1984). Furthermore, our results do not necessarily indicate competition for food between the catfish species, as we recorded evidence of trophic niche partitioning among adults and between females (Fig. 4). Previous studies have documented food resource partitioning among Heptapteridae species (Brazil-Sousa et al. 2009; Silva et al. 2012; Bonato and Fialho 2014). Microhabitat segregation was also observed in the area: *R. guatemalensis* occurs in pools or rivers with slow currents and plant material such as algae, trunks, leaves and branches, while *R. laticauda* is found in rocky riffles and stream currents (Julián-Caballero et al. 2023). Similar microhabitat segregation has been reported for these species in Colombia (Hernández et al. 2015). However, it is imperative to conduct studies on spatial niche dimension (see Ferreira et al. 2023) to verify if partitioning occurs in this dimension (Schoener 1974).

These two species show overlapping distributions in the Neotropical region (Miller 1984; Perdices et al. 2002; Hernández et al. 2015) and can probably coexist in rivers as long as there are optimal conditions for both. Future studies should include an analysis of prey availability in the habitat where *Rhamdia* species occur. This will help assess their electivity (Vanderploeg and Scavia 1979) and provide a greater understanding of their feeding strategies.

Conclusion

Rhamdia guatemalensis and *R. laticauda* differ in standard length and weight, which could avoid direct overlap in food usage. Our result highlights the fundamental role of these species in the area as carnivores and biological controls for Diptera, Ephemeroptera, and Megaloptera. Our quantitative analysis of stomach contents allows us to classify the two species as aquatic invertivores and potential predators. The diet of both species varies in composition according to size and shows sexual differentiation for *R. guatemalensis*. Both species are secondary consumers and tend to specialize in consuming insects. We also provide evidence that adults and females consume different prey orders, enabling closely related species to coexist through trophic partitioning. This information is essential for understanding the tropic ecology of two *Rhamdia* species that coexist in the TCBR and could be crucial for developing conservation and management plans for these nocturnal predator fishes in a protected natural area of Mexico.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CCJC, ECA, RMGU, EMR. Data curation: CCJC, EMR. Formal analysis: CCJC. Funding acquisition: EMR. Investigation: CCJC, ECA. Methodology: CCJC, EMR. Project administration: EMR. Resources: EMR. Software: CCJC. Supervision: ECA, EMR, RMGU. Validation: EMR, CCJC, RMGU, ECA. Visualization: RMGU, CCJC, EMR. Writing - original draft: CCJC. Writing - review and editing: RMGU, ECA, EMR, CCJC.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

List of specimens with voucher codes, locality information, and body measurements

Authors: César Camilo Julián-Caballero, Emilio Martínez-Ramírez, Rosa María Gómez-Ugalde, Eufemia Cruz-Arenas

Data type: xlsx

Explanation note: List of specimens with voucher codes (CIDOAX), locality information (MEX), and body measurements: Total length, Standard length, and Body weight using in this manuscript taken from Collection of Continental Fish at the CIIDIR Unidad Oaxaca IPN, Mexico (OAX.PEC.122.0302).

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Link: https://doi.org/10.3897/neotropical.19.e119908.suppl1

Supplementary material 2

Foods identified in the digestive tracts of *Rhamdia guatemalensis*

Authors: César Camilo Julián-Caballero, Emilio Martínez-Ramírez, Rosa María Gómez-Ugalde, Eufemia Cruz-Arenas

Data type: xlsx

Explanation note: Foods identified in the digestive tracts of *Rhamdia guatemalensis* (n = 72). AP = autochthonous prey, ALP = allochthonous prey, B = benthic prey; C = prey preferring the water column. Stage L = Larva, P = Pupa, N = Nymph, AD = Adult. J = juveniles, and Ind = Indeterminate prey.

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Link: https://doi.org/10.3897/neotropical.19.e119908.suppl2

Supplementary material 3

Foods identified in the digestive tracts of *Rhamdia laticauda*

Authors: César Camilo Julián-Caballero, Emilio Martínez-Ramírez, Rosa María Gómez-Ugalde, Eufemia Cruz-Arenas

Data type: xlsx

Explanation note: Foods identified in the digestive tracts of *Rhamdia laticauda* (n = 112). AP = autochthonous prey, ALP = allochthonous prey, B = benthic prey; C = prey preferring the water column. Stage L = Larva, P = Pupae, N = Nymph, AD = Adult. J = Vertebrate juveniles, and Ind = Indeterminate prey.

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Link: https://doi.org/10.3897/neotropical.19.e119908.suppl3

Supplementary material 4

Percentage of ocurrence, percentage number, and percent weight of stomach content data

Authors: César Camilo Julián-Caballero, Emilio Martínez-Ramírez, Rosa María Gómez-Ugalde, Eufemia Cruz-Arenas

Data type: xlsx

Explanation note: Percentage of ocurrence, percentage number, and percent weight of stomach content data of two *Rhamdia* species for calculated the Index of Relative Importance.

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